BIOLOGICAL OXIDATION AND REDUCTION OF INORGANIC COMPOUNDS OF SULFUR

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The biological processes involved in the oxidation and reduction of inorganic compounds of sulfur are generally represented by the idealized "biological sulfur cycle" shown in Figure 1 (18). Sulfate and sulfide are pivotal compounds in the scheme as they represent both the most common forms of inorganic sulfur found in nature and are the most common forms of sulfur incorporated into biological materials. At the top of the scheme, the biosynthetic reactions involving the incorporation of sulfate as ester linkages into carbohydrates, lipids, phenol, steroids, etc. (14) are indicated as sulfation reactions. Sulfation reactions are extensively involved in the biosynthesis of structural components in plants and animals but sulfate esters have only rarely been reported to occur in bacteria. All three groups of organisms do have sulfatases which specifically hydrolyze the various esters. On the right hand portion of the scheme, the eight electron reduction of $SO_4^{=2}$ to S^{-2} is represented and, at the bottom of the scheme, the biosynthesis of amino acids and cofactors (or vitamins) from S^{-2} is shown. On the left hand portion of the scheme, the oxidation of reduced sulfur compounds is indicated (shown here as sulfide but other common substrates include $S_2O_3^{=2}$ and elemental sulfur). The biological aspects of inorganic sulfur metabolism thus provide the essential transformations for the incorporation of sulfur into biological materials and a link between the appropriate geological and biological phenomena.

The oxidative and reductive process have been further classified depending on the organisms and the physiological significance of the process in their metabolism. Two physiological types of sulfate reduction are recognized (21). The first is assimilatory or biosynthetic sulfate reduction in which organisms reduce only enough sulfate to meet their nutritional requirements for sulfur. This pathway is considered to be in the pathway for the biosynthesis of cysteine and is usually under both coarse and fine metabolic regulation (29). Animals do not classically reduce sulfate and must depend upon plants and bacteria for their metabolites containing reduced sulfur. This pathway occurs in most plants and bacteria, including aerobes and anaerobes, and, because of its wide occurrence, is probably the largest biological process for the reduction of sulfate; however, only indirectly during the digestion and hydrolysis of biological materials does this pathway produce sulfide in nature. The second sequence involved in the reduction of sulfate is the dissimilatory or respiratory pathway of sulfate reduction in which sulfate in the absence of oxygen serves as a terminal electron acceptor for anaerobic respiration (13). This pathway of sulfate reduction occurs only in the sulfate-reducing bacteria, species of *Desulfovibrio* (25) and *Desulfotomaculum* (4), and results in the formation of very large amounts of S^{-2}. Respiratory sulfate reduction is the process responsible for the formation and accumulation of most S^{-2} in nature and is believed to be involved in many geochemical phenomena. The enzymes of the respiratory pathway are constitutive, i.e. not effected by growth conditions, and the intermediates and enzymes responsible for respiratory sulfate reduction are quite different from those involved in biosynthetic sulfate reduction. Members of the genus, *Desulfovibrio* are the most extensively studied of the sulfate-reducing bacteria. These bacteria have only a limited capability for oxidizing substrates (H_2, formate, pyruvate, lactate, ethanol, fumarate) and are the first non-photosynthetic anaerobes in which c-type cytochrome were discovered (24). They also produce many low molecular weight electron carriers (13) and oxidative phosphorylation has been demonstrated to be coupled to electron transfer (19).

Most plants, bacteria and animals are capable of oxidizing reduced inorganic and organic compounds of sulfur to sulfate. Thus, a specific requirement of sulfate for growth has never been reported although it is extensively involved in essential biosynthetic reactions in plants and animals. Reduced sulfur compounds can also be utilized by microorganisms as electron donors for both aerobic and anaerobic growth, as well as photosynthetic growth with the formation of sulfate. Members of the genus, Thiobacillus, oxidize S^{-2}, $S_2O_3^{=2}$ and S° to $SO_4^{=2}$ in the presence of oxygen and gain energy for growth in the form of adenosine triphosphate (ATP) by means of oxidative phosphorylation (32). One species, T. denitrificans can utilize either oxygen or nitrate with the formation of N_2 as terminal electron acceptor. Photosynthetic bacteria, members of the Chromatiaceae (purple sulfur bacteria) and Chlorobiaceae (green sulfur bacteria) can use reduced sulfur compounds as electron donors for photosynthetic growth first with the formation of S° and subsequently $SO_4^{=2}$. Although the biological sulfur cycle generally involves a large number of diverse organisms, it is possible to construct a simple, light-driven sulfur cycle by means of a sulfate-reducing bacterium and a photosynthetic bacterium. This is not a primary producing system, as water can not serve as a source of electrons, but it provides a model system for the study of the interactions required for the biological sulfur cycle. In addition, this simple form of the cycle may represent a primitive system for the conversion of solar energy into biologically useable energy.

In most soils and natural environments, there is a continuous flux of sulfur through the biological sulfur cycle without the accumulation of intermediates or significant changes in the concentrations of sulfate and sulfide. This situation can then be regarded as an uninterrupted or continuous sulfur cycle. Under certain conditions, one or more steps in this sulfur cycle can become inhibited with the result that the concentrations of sulfate and sulfide are drastically altered, often with dramatic effects on a specific environment. This can be considered to be an interrupted or discontinuous sulfur cycle and its consequences will be briefly considered. Under anaerobic conditions, the oxidation of reduced sulfur compounds is inhibited (except in the presence of NO_3^{-1}) and, with $SO_4^{=2}$, organic electron donors or H_2 and an environmental pH above 4.5, copious amounts of S^{-2} can be produced by the sulfate reducing bacteria. The consequences of this microbial reduction of sulfate to an environment are complex but can be largely analyzed in terms of the chemical properties of H_2S. Sulfide is an inhibitor of cytochrome oxidase which is essential for aerobic respiration, reacts with molecular oxygen and generates a reducing environment because of its low E_u value of about -300 mV. Thus, its formation in any environment can result in the formation of anaerobic conditions and the inhibition of aerobic flora. Sulfide also combines with heavy metals present in an environment to form insoluble sulfides and there is some evidence to indicate that most pyrite ores are formed from biologically produced sulfide. The black color of anaerobic environments is due to this reaction and the Black Sea is claimed to derive its name from the fact that in areas it appears to be black due to the abundance of FeS. As indicated previously, sulfide and elemental sulfur can serve as substrates for the growth of many microorganisms and on the periphery of an environment in which there is extensive sulfate reduction (termed a "sulfuretum") one can often find high concentrations of Thiobacilli and/or photosynthetic bacteria. For example, in very shallow marine environments, it is common to observe red and green photosynthetic bacteria growing on the surface of sediments that are producing S^{-2}. This phenomenon is made possible in part because at physiological pH values, H_2S is volatile and a sulfuretum can usually be detected by our olfactory senses. The volatility of H_2S formed by sulfate reduction can also result in an environment becoming extremely alkaline and it has been postulated to be the cause of the formation of certain deposits of Na_2CO_3 by the absorption of CO_2 from the atmosphere. The concentration of sulfate can be decreased in natural waters to the point that respiratory sulfate reduction ceases and interactions with methanogenic bacteria become important as will be discussed later. The sulfate-reducing bacteria have high levels of the enzyme hydrogenase concentrated around the periphery of their cells (18) and the enzyme appears to be important both in the production and utilization of molecular hydrogen which is commonly found in anaerobic environments. The ability to utilize extremely low concentrations of H_2 has been postulated to be the role of the organisms in the rapid anaerobic corrosion of iron (9). The various environmental aspects of respiratory sulfate reduction are summarized in Table 1 and most of these environmental

TABLE 1: Environmental Effects of Respiratory Sulfate Reduction

1. Formation of Sulfide
2. Change of pH
3. Removal of Heavy Metals
4. Removal of Hydrogen
5. Removal of Sulfate
6. Changes in Microflora
7. Fractionation of Sulfur Isotopes

effects of respiratory sulfate reduction can be interpreted in terms of the chemical, biological and physical properties of H_2S. Postgate (23) has presented a more detailed and extensive discussion of these environmental effects of sulfate reduction. A related aspect of these bacteria is the fractionation of sulfur isotopes occurring during the reduction of sulfate which allows determination as to whether a given deposit of reduced sulfur was formed by geological phenomena or biological agents (34).

Under aerobic conditions, the absence of organic electron donors and/or acidic pH values (below 4.5) respiratory sulfate reduction is inhibited and a second type of imbalance in the biological sulfur cycle created which leads to the formation of very acidic environments (to pH 1.0). For this situation to occur, the presence of reduced sulfur compounds, such as H_2S, S° or $S_2O_3^{-2}$, which can be oxidized by the Thiobacilli to sulfate as H_2SO_4, is required. In contrast to the sulfate-reducing bacteria which require fixed carbon, these organisms can utilize CO_2 as their sole source of carbon (35). This acidic environment occurs particularly where there is poor drainage and its formation can inhibit the growth of a wide variety of soil bacteria. From an economic point of view, these microorganisms can be important agents in the erosion of various types of stone and this aspect is emphasized by one isolate of these bacteria being named *T. concretivorous* (17). In general, the various physiological types of microorganisms responsible for the oxidation and reduction of inorganic sulfur compounds have been isolated in pure culture and their physiology studied sufficiently to predict and control the accumulation of sulfide and sulfate in a given environmental situation.

The biochemistry of the reactions of inorganic sulfur compounds has been only sporadically studied but although not all of the enzyme and reactions have been completely characterized, the reactions involved can at least be reasonably well outlined. Sulfate is first transported across the membrane of the cell by means of an active process involving sulfate-binding proteins (16) and once inside the cell universally reacts with ATP to form adenylyl sulfate (APS) and inorganic pyrophosphate (PP_i) as shown in Table 2, reaction 1. The equilibrium of the reaction lies in the direction of ATP and SO_4^{-2} and, for significant formation of APS, the reaction must be coupled to either or both pyrophosphate hydrolysis, Table 2, reaction 2, or phosphorylation in the 3'-position to form 3'-phosphoadenylyl sulfate (PAPS), Table 2, reaction 3. PAPS serves as the substrate for all sulfation reactions, Table 2, reaction 4, and forms a sulfate ester and 3',5'diphosphoadenosine (PAP), but specific enzymes, termed sulfotransferases, are required for the various acceptors such as alcohols, phenols, steroids, etc. PAPS is also believed to be the form in which SO_4^{-2} is reduced to SO_3^{-2} by the reduced triphosphopyridine nucleotide ($TPNH_2$) specific PAPS reductase Table 2, reaction 5; but, the role of this enzyme and that of the $TPNH_2$: sulfite reductase, Table 2, reaction 6, which catalyzes the 6 electron of SO_3^{-2} to S^{-2} in the biosynthetic pathway has recently been questioned (30). However, it remains clear that the biosynthetic pathway is biochemically distinct from the respiratory pathway.

TABLE 2: The Enzymes of Biosynthetic Sulfate Reduction

1. ATP:sulfurylase

$$ATP + SO_4^{-2} \xrightarrow{Mg^{+2}} APS + PP_i \qquad (28)$$

2. Inorganic pyrophosphatase

$$PP_i + H_2O \xrightarrow{Mg^{+2}} 2P_i \qquad (28)$$

3. APS:kinase

$$ATP + APS \xrightarrow{Mg^{+2}} PAPS + ADP \qquad (27)$$

4. Sulfotransferase

$$ROH + PAPS \rightarrow ROSO_3^{-1} + PAP \qquad (14)$$

5. PAPS reductase

$$PAPS + TPNH_2 \rightarrow SO_3^{-2} + PAP + TPN \qquad (37)$$

6. Sulfite reductase

$$SO_3^{-2} + 3TPNH_2 \rightarrow S^{-2} + 3TPN + 3H_2O \qquad (31)$$

The initial step in the respiratory pathway of sulfate reduction is the same as that in the biosynthetic pathway, that is, the formation of APS from ATP and SO_4^{-2} by ATP sulfurylase and its formation is coupled only to the hydrolysis of inorganic pyrophosphate, Table 2 and 3, reactions 1 and 2. APS rather than PAPS is the form

TABLE 3: The Enzymes of Respiratory Sulfate Reduction

1. ATP:sulfurylase

$$ATP + SO_4^{-2} \rightarrow APS + PP_i \qquad (28)$$

2. Inorganic pyrophosphatase

$$PP_i + H_2O \rightarrow 2P_i \qquad (28)$$

3. APS:reductase

$$APS + 2e \rightarrow AMP + SO_3^{-2} \qquad (20)$$

4. Bisulfite reductase

$$HSO_3^{-1} + 2e + 3H^+ \rightarrow S_3O_6^{-2} + 3H_2O \qquad (11)$$

5. Trithionate reductase

$$S_3O_6^{-2} + 2e \rightarrow S_2O_3^{-2} + SO_3^{-2} \qquad (10)$$

6. Thiosulfate reductase

$$S_2O_6^{-2} + 2e \rightarrow S^{-2} + SO_3^{-2} \qquad (8)$$

in which SO_4^{-2} is reduced to SO_3^{-2} with the formation of AMP, Table 3, reaction 3, by APS reductase in a reversible oxidation-reduction reaction. Sulfite (or bisulfite) is not directly reduced to S^{-2} by a single enzyme as in the biosynthetic pathway but rather three separate reductive steps are involved. In a complex reaction involving three molecules of sulfite, SO_3^{-2} is reduced to trithionate ($S_3O_6^{-2}$) by a hemoprotein, bisulfite reductase, of which there are three different types, desulfoviridin, desulforubidin (12) and P582 (1), Table 3, reaction 4. Trithionate is next reduced to thiosulfate with the concomitant formation of sulfite by trithionate reductase, Table 3, reaction 5. The thiosulfate is then reductively cleaved to yield S^{-2} and a second molecule of SO_3^{-2}, Table 3, reaction 6. The electron donors for these reductions have not been definitively established but they appear to be low-molecular weight electron transfer proteins. In both pathways, the result is identical in that SO_4^{-2} is reduced to S^{-2}; however, the respiratory pathway requires one less ATP and four discrete reductive steps rather than the two involved in the biosynthetic pathway. These differences probably reflect the different physiological roles of the pathways.

The respiratory pathways involved in the oxidation of reduced sulfur compounds to SO_4^{-2} are less well defined than those in the reduction of sulfate. The key reaction is the oxidation of a cofactor or enzyme-bound polysulfide (15) to sulfite in an oxygen requiring oxidation, Table 4, reaction 1 (33). Elemental sulfur and

TABLE 4: The Reactions of Respiratory Sulfur Oxidation

1. Polysulfide oxidase		
	$H_2O + RS_nSS^- + O_2 \rightarrow RS_nS^{-1} + SO_3^{-2} + 2H^+$	(33)
2. Thiosulfate formation		
	$S^\circ + SO_3^{-2} \rightarrow S_2O_3^{-2}$	(33)
3. Thiosulfate reductase		
	$2e + S_2O_3^{-2} \rightarrow SO_3^{-2} + 2S^{-2}$	(22)
4. Sulfite oxidase		
	$SO_3^{-2} + 1/2\ O_2 \rightarrow SO_4^{-2}$	(6)
5. APS reductase		
	$AMP + SO_3^{-2} + 2\ \text{cyto}\ c_{ox} \rightarrow APS + 2\ \text{cyto}\ c_{red}$	(22)
6. ADP sulfurylase		
	$APS + P_i \rightarrow ADP + SO_4^{-2}$	(22)

sulfide can form this "bound polysulfide" (R) and thus enter the reaction sequence; however, little is known about the details of these interactions. Sulfite is a highly reactive molecule and non-enzymatically combines with elemental sulfur to form thiosulfate, Table 4, reaction 2. Thiosulfate is returned to the main respiratory pathway by reductive cleavage to sulfide and sulfite by thiosulfate reductase, Table 4, reaction 3. The final step is the oxidation of SO_3^{-2} to SO_4^{-2} and is accomplished by two enzymatic pathways. The first is the simple oxidation of SO_3^{-2} to SO_4^{-2} by the enzyme, sulfite oxidase, in certain of the Thiobacilli, Table 4, reaction 4. This oxidase has been reported to be absent in the photosynthetic bacteria (36). The second pathway, found in the photosynthetic bacteria and some of the Thiobacilli, involves the oxidation of SO_3^{-2} in the presence of AMP to the level of sulfate as APS by APS reductase, Table 4, reaction 5. The high energy sulfate can then be exchanged for a phosphate group to yield ADP by the enzyme, ADP:sulfurylase to produce biologically utilizable energy, Table 4, reaction 6. Thus, microorganisms utilizing the APS pathway are able to obtain energy by means of a substrate phosphorylation in addition to either oxidative phosphorylation or photophosphorylation. In all considerations of the biological sulfur cycle, it must be borne in mind that the oxidation of reduced sulfur compounds yields energy and that the reduction of sulfate requires energy although the reduction of sulfate can be coupled with an oxidative reaction which produces more energy than the reduction of SO_4^{-2} requires and thereby produce energy for growth.

An important aspect of the biological sulfur cycle is the ability of certain of these anaerobic microorganisms to link and thereby modify their fermentative respiratory pathways by means of the intracellular transport or transfer of molecular hydrogen. This linking of fermentations allows these anaerobic bacteria to grow under some unexpected and surprising conditions in an almost symbiotic relationship. There are now several well documented examples of this biological phenomenon. Methanobacillus omelianskii has been demonstrated to be a mixed culture growing in this type of relationship and forming acetate and CH_4 from CO_2 and ethanol (3). One of the organisms, the S organism, oxidizes ethanol to acetate and H_2 but grows poorly. The second organism, the H organism, reduces CO_2 to CH_4 with H_2 and appears to "pull" the oxidation of ethanol to acetate by the oxidation of H_2 as growth is greater in the mixture than in pure culture (26). Chloropseudomonas ethylica has been demonstrated to be a mixed culture which photosynthetically oxidizes ethanol to acetate (7). The culture consists of a sulfate-reducing bacterium which oxidizes ethanol to acetate with the reduction of SO_4^{-2} to S^{-2} as shown in Eq. 1.

$$2CH_3CH_2OH + SO_4^{-2} \rightarrow 2CH_3COOH + S^{-2} + 2H_2O \qquad 1)$$

and a green sulfur bacterium which photosynthetically oxidizes S^{-2} to SO_4^{-2} as shown in Eq. 2.

$$2CO_2 + S^{-2} + 2H_2O \xrightarrow{hv} SO_4^{-2} + 2CH_2O \qquad 2)$$

The possible involvement of intercellular H_2 transfer in this relationship has not yet been resolved. A third example involves an obligatory relationship between a sulfate-reducing bacterium and a methanogenic bacterium. Sulfate (or fumarate) is obligatory for the growth of species of Desulfovibrio on lactate as shown in Eq. 3.

$$2\ \text{lactate} + SO_4^{-2} \rightarrow S^{-2} + 2\ \text{acetate} + 2CO_2 + 2H_2O + 2H^{-1} \qquad 3)$$

Recently, it has been demonstrated that the sulfate-reducing bacteria can oxidize lactate to ethanol when grown in the presence of methanogenic bacteria and the electrons (as H_2) utilized for the reduction of CO_2 to CH_4 rather than the reduction of SO_4^{-2} to S^{-2} (2). This relationship involving intercellular H_2 transfer is shown in Eqs. 4, 5 and 6.

Sulfate reducing bacterium

$$2CH_3CH_2OHCOOH + 2H_2O \rightarrow 2CH_3COOH + 2CO_2 + 4H_2 + 2H^+ \qquad 4)$$

Methanogenic bacterium

$$4H_2 + CO_2 \rightarrow CH_4 + 2H_2O \qquad 5)$$

Sum:

$$2CH_3CH_2OHCOOH \rightarrow 2CH_3COOH + CO_2 + CH_4 + 2H^+ \qquad 6)$$

In essence, CO_2 is functioning as electron acceptor for the fermentation of lactate (and probably other electron donors) and H_2 is transferred between these two anaerobic but physiologically different types of bacteria. The mechanism of this relationship has been postulated to be the "pulling" of lactate oxidation by the utilization of H_2 for CH_4 formation. This concept is also supported by the observation that hydrogenase is concentrated around the outside of the sulfate-reducing bacteria. Thus, methane formation is operating as an "electron sink" or terminal oxidase and could conceivably be "pulling" the complex series of fermentative reactions occurring in the cellulose breakdown.

The observations offer a new theoretical basis for the interpretation of a portion of the microbiology and biochemistry in anaerobic sediments of fresh and marine waters. Intercellular H_2 transfer appears to be a specific adaptation of anaerobic bacteria which allows them to greatly extend their growth potential. Thus, the number of physiological types of microorganisms involved in the transformation of organic materials may be far fewer than previously anticipated. The ideas also suggest that a specific environment may have unexpected potential for microbial activities such as sulfate reduction, hydrogen utilization or nitrate reduction. It has also recently been established that anaerobic sediments are stable enough so that classical biochemical and physiological experiments can be performed with sediments by treating them as bacterial cultures (5). Investigations utilizing these two concepts should lead to a much greater understanding of the reactions occurring in organic deposits and indicate the ways in which these complex fermentations can be applied to specific problems of economic concern.

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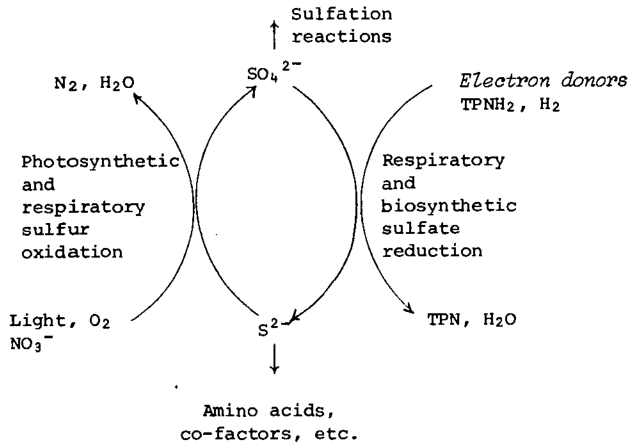

Fig. 1. A simple representation of the biological sulfur cycle.